

MORPHOLOGICAL STRUCTURE AND FUNCTION IN DESERT HETEROMYID RODENTS¹

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ABSTRACT.— The functional morphology of desert heteromyid rodents (*Perognathus*, *Dipodomys*, *Microdipodops*) is reviewed with considerable new information provided. Specific attention is given to the interaction of anatomical structure and the behavioral and ecological patterns of these rodents.

Inflation of the auditory bullae, although apparently related to improved hearing, is also shown to directly impact the structure and function of the feeding apparatus in desert heteromyids. The mechanics of high speed seed punching behavior in *Dipodomys deserti* as well as the rates of digging activities of various heteromyids are described using data from slow motion films. The biomechanical consequences of cheek pouch loading for body size and locomotor behavior yield theoretical predictive models concerning interspecific differences in foraging behavior, dietary preference, and microhabitat selection.

Structural modifications of the forelimb associated with use of external cheek pouches reduce the mechanical competence of these limbs for shock absorption during fast quadrupedal running. The relative size of various front and hind limb segments are correlated with quadrupedal, tripodal, and bipedal gaits in heteromyid rodents. The interdependence of body balance, gait, and speed are examined in *Dipodomys merriami*. Factors possibly contributing to the origin of bipedalism in rodents are reviewed and discussed.

The heteromyid rodents of North America offer, potentially, a superb opportunity to examine the importance of morphological design as a determinant of behavioral and ecological patterns under natural conditions. This follows from the considerable range of morphologies found within this circumscribed group as well as the impressive breadth of habitats that its living representatives presently occupy. Perhaps more significant is the fact that heteromyids have recently become the focus of numerous investigations aimed at gaining a better understanding of their biology on multiple levels (e.g., physiology, behavior, ecology, community level interactions). Such studies have begun to offer the kinds of information against which carefully framed hypotheses of a functional-morphologic nature might be critically appraised.

Earlier morphologic studies on heteromyids are primarily descriptive but also contain comments on form-function relationships that are, of necessity, relatively superficial and speculative. Excellent works of this type are Howell's (1932) monograph on the myology and osteology of *Dipodomys*, Hatt's

(1932) comparative study of vertebral architecture in saltatorial rodents, and Wood's (1935) important survey of the fossil and Recent Heteromyidae. Berman's (1979) recent multivariate statistical analysis of hind limb bone and muscle morphology in bipedal rodents constitutes a very significant extension beyond the older comparative anatomical works.

Recent functional morphologic studies have been more analytical and experimental, but also of more limited scope. Thus, Pinkham (1976) has investigated the gaits and mechanics of quadrupedal and bipedal running in *Liomys* and *Dipodomys* by combining high speed cinematography with force platform recordings. Using similar techniques, but also including cineradiography, Biewener et al. (1981) have studied the mechanical behavior of the major hindlimb tendons in kangaroo rats. Additional information on the ankle mechanics of *Dipodomys* and the physiological properties of its associated musculature has been presented by Williamson and Frederick (1977). Kaup (1975) has also commented on the biomechanical and evolutionary significance of hind limb anatomy in heteromyids.

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Of special note are the investigations of the Websters (see below) on the auditory apparatus of heteromyids. Not only have their studies provided a large body of comparative morphologic data, but they also offer one of the few examples wherein specific hypotheses concerning the adaptive value of a major morphological complex have been tested.

In the present paper we briefly review the existing data on the functional morphology of heteromyid rodents and point out significant gaps in our knowledge. Considerable attention is given the forelimbs and cheek pouches, two structures that have received little attention in the past but whose structural organization may place important constraints on the behavior of these animals. Here and elsewhere we have tried to show how functional morphologic analyses can lead to predictive, testable models concerning the natural behavior and ecology of heteromyid rodents.

Limitations of both time and materials have forced us to restrict the present discussion to "desert heteromyids" of the genera *Perognathus*, *Dipodomys*, and *Microdipodops*. This is done with full knowledge that a better understanding of the functional anatomy and behavior of the modern heteromyines (*Liomys*, *Heteromys*) would undoubtedly broaden our appreciation of form-function and evolutionary patterns within perognathine and dipodomysine heteromyids and might well alter some of our conclusions.

SKULL AND NECK MORPHOLOGY

Skull

The most striking cranial feature of desert heteromyids and that which has received the most attention is the enlarged middle ear chambers or auditory bullae. The auditory bullae are moderately inflated in *Perognathus*, but grossly so in both *Dipodomys* and *Microdipodops* (Fig. 1). Relative to overall head size, the middle ear chambers achieve their greatest volume in the latter genus (Webster 1961). Detailed comparative morphologic data on the auditory region of heteromyids have been provided by Webster and Webster (1975, 1977, 1980).

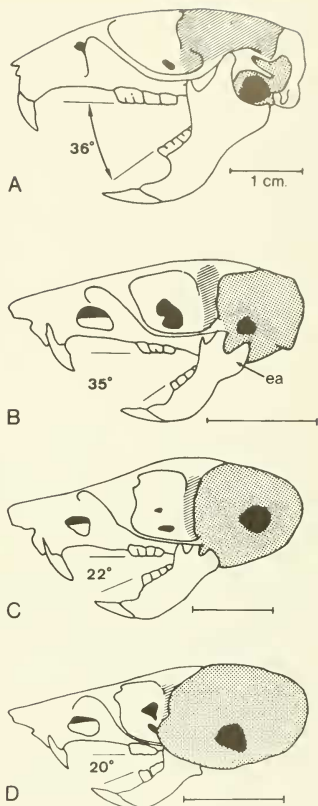


Fig. 1. Influence of auditory specialization on the feeding apparatus of desert heteromyids. A generalized desert rodent, *Neotoma lepida* (A) is compared to *Perognathus fornosus* (B), *Dipodomys merriami* (C), and *Microdipodops megacephalus* (D). Inflation of the auditory bulla (stippled) reduces the area of origin of the temporalis musculature (hatched) and also restricts gap by crowding the mandible from behind. The specialized everted angle (ea) of the mandible reduces the impact of bullar inflation in heteromyids. Maximum gap between the cheek teeth (but not incisors) in *Perognathus* (35°) is about equal to that in *Neotoma* (36°), but extreme middle ear hypertrophy has severely reduced gap in *Dipodomys* and *Microdipodops*. All skulls drawn to same length.

The innovative studies of the Websters and their collaborators have gradually revealed the functional and probable adaptive significance of the modified ears of desert hetero-

myids. Auditory specializations in these rodents, and in certain Old World desert species (Lay 1972), improve the detection of relatively low frequency sound, especially in the 1-3 KHz range. Selective sensitivity to these frequencies has been established on the basis of physiological (Ruppert and Moushegian 1970, Vernon et al. 1971, Webster and Strother 1972, Webster and Webster 1972) and behavioral experiments (Webster and Webster 1972). A suite of structural features appear to be responsible for increased sensitivity to low frequency sound by lowering impedance and, hence, increasing the transmission of such sound from the external to inner ear. Among these features are: (1) a relatively large, compliant tympanic membrane; (2) a small, low-mass, high-leverage ossicular chain; and (3) an enlarged middle ear chamber. The latter feature is apparently a compensatory adjustment that reduces middle ear damping of the large ear drum (Legoux et al. 1954, Webster 1962, Wisner et al. 1954). Experimental reduction of middle ear volume in kangaroo rats significantly reduces sensitivity to low frequency sound (Webster 1961, Webster and Webster 1972, 1980). Certain structural modifications of the inner ear (Webster 1961, Webster and Stack 1968) and related areas of the brain (Webster et al. 1968) may also reflect selective sensitivity to low frequency sound in *Dipodomys*.

How the specialized ears of kangaroo rats might contribute to individual fitness has also been examined. Captive kangaroo rats (*D. merriami*) were tested to see how effectively and by what means they avoided the attacks of owls and rattlesnakes (Webster 1962, Webster and Webster 1971). Animals with unimpaired hearing were usually able to avoid capture by these predators even in total darkness or when blinded. Those with impaired hearing (i.e., artificially reduced middle ear volumes) could also avoid attack, but only when there was sufficient light to see the movements of the predator. Blind kangaroo rats with impaired hearing could not escape predation. A comparison of mortality rates between *Dipodomys* with normal and impaired hearing under field conditions suggests higher mortality among impaired animals, especially during dark of the moon intervals (Webster and Webster 1971). It is

presumed that mortality was due chiefly to higher rates of predation upon kangaroo rats whose ability to detect low frequency sound had been reduced. Laboratory recordings indicate that the predatory strikes of both owls and rattlesnakes produce significant sound in the 1-3 KHz range (Webster 1962). In sum, the available data strongly imply that the specialized auditory apparatus of desert heteromyids is indeed adaptive, and that it may confer its greatest advantage on individuals foraging under conditions of dim illumination.

There has been little functional analysis of the feeding mechanism of heteromyid rodents. Most studies have been concerned with dental morphology as it relates to systematics and the identification of fossil materials (Lindsay 1972, Shotwell 1967, Wood 1935). The cheek teeth of modern desert heteromyids are relatively simple and lophodont. In *Dipodomys* the cheek teeth are hypsodont and rootless. Enamel is confined to the anterior and posterior faces, a condition paralleled in the Geomyidae (Wood 1937). The mandible tends to be small (relative to head size) in all living heteromyids, but is markedly so in *Dipodomys* and *Microdipodops*. The smallness of the mandible causes it to be rather severely underslung. This position, together with the dorsal location of the eyes (Howell 1932), assures that the movements of the hands during feeding and pouching behavior are kept well below eye level.

Inflation of the middle ear has impinged directly on the masticatory apparatus by (1) forcing a reduction of the temporalis musculature and (2) crowding the mandible from behind, thereby placing serious limitations on gape. The latter problem has been partially circumvented by the development of an everted angular process. Reorientation of the angular process delays its contact with the undersurface of the bulla as the jaw is opened (depressed). This permits a wider gape than would otherwise be possible. Even so, middle ear inflation restricts gape in all desert heteromyids, but most especially in *Dipodomys* and *Microdipodops* (Fig. 1). A restriction in gape will limit the size of resistant food items that an animal can effectively gnaw. Exactly how restructuring of the posterior region of

the lower jaw has influenced other biomechanically important descriptors of masticatory function (e.g., force, rate, and direction of mandibular movements; organization of adductor musculature) is unknown at this time.

Another prominent feature of the cranium of desert heteromyids is the strongly projecting, tubular nasal region. The nasal passage is occupied by closely spaced turbinate bones. The length of the nasal passage as well as the diameter of its individual air channels are presumably important to the water conserving, counter-current heat exchanger possessed by *Dipodomys* (Jackson and Schmidt-Nielsen 1964, Schmidt-Nielsen et al. 1970). The relative development of the nasal region in desert heteromyids as regards their ability to detect subsurface accumulations of seeds (Frye and Rosenzweig 1980, Reichman 1979) merits examination.

The interior of the skull of desert heteromyids exhibits at least one obvious specialization. Well-formed bony partitions project medially from the otic capsules into the space between the cerebral and cerebellar lobes of the brain. They are pronounced in *Dipodomys* and *Microdipodops*, but more modestly developed in *Perognathus*. These partitions, which tend to compartmentalize the brain within the cranium, appear to be true tentorial ossifications. As such they cannot be directly related to inflation of the middle ear. Whether or not such structures have any functional connection with the rapid accelerations of the head and brain experienced by bipedal heteromyids invites investigation.

Neck

Hatt (1932) described vertebral modifications that seem to be associated with bipedal saltation in rodents. Among them are: (1) extreme shortening and compaction of the cervical region, (2) pronounced dorsiflexion (= hyperextension) of the neck, and (3) partial or complete fusion of the anterior (excluding atlas) neck vertebrae. These specializations are common to both Old World (Dipodidae, Pedetidae) and New World (Heteromyidae) bipeds, but are most pronounced in *Jaculus*, *Dipus*, and *Dipodomys* (Hatt 1932).

Reorganization of the cervical region appears to accomplish two functions. First, it helps to foreshorten the anterior trunk, which tends to keep the distribution of body mass rearward. This eases the problem of counterbalancing the body over the hind limbs when in the bipedal pose. Secondly, modifications of the neck increase its mechanical strength and stability while the animal is involved in bipedal hopping. Hatt (1932) argued that neck specialization was required to reduce bobbing of the head. This idea has been accepted by many subsequent workers, but has never been experimentally verified. Hatt himself offered no functional analysis in support of his model.

CHEEK POUCHES

Structure, Use and Significance

External, fur-lined cheek pouches are a unique, derived feature of geomyoid rodents. They are not present at birth, but rapidly develop during the early postnatal period from infoldings of the facial skin (Lackey 1967). In the adult, each pouch opens externally via a long slitlike aperture. Internally, the pouch continues rearward to an expanded base that rests over the shoulder blades. Geomyids can voluntarily evert the pouches for cleaning (Vaughan 1966) and perhaps in some cases to help empty their contents. In both geomyids and heteromyids superficial facial musculature is used to control the tension in the skin guarding the entrance to the pouch and a special "pouch muscle," derived (in part) from the trapezius complex, returns the everted pouch to its normal position (Chiasson 1954, Hill 1937, Howell 1932).

Two fairly obvious advantages of cheek pouches are (1) reducing the time required to gather food on the surface, hence reducing exposure to predators and, (2) reducing the locomotor energy expended in foraging, by allowing an animal to collect and store a given amount of food with fewer trips. The latter may be especially important where food resources tend to be widely scattered (Reichman and Oberstein 1977). Another possible advantage of external cheek pouches to desert heteromyids is that of water conservation. Unlike internal cheek pouches (independently evolved in many mammalian

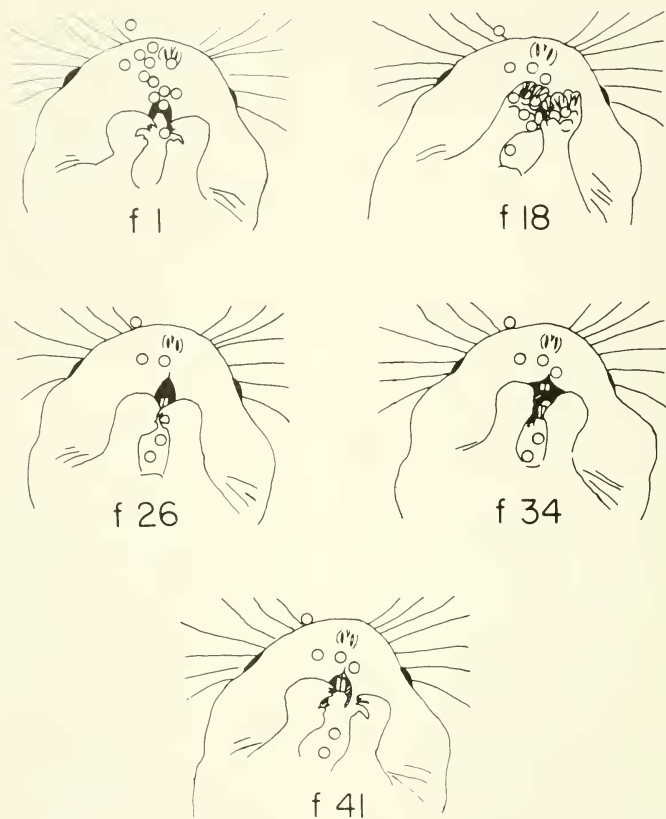


Fig. 2. Seed pouching in *Dipodomys deserti*. Tracings of representative frames of slow motion film (200 fps) of *D. deserti* illustrate one complete pouching cycle. Millet seed and the kangaroo rat were placed on a glass surface and filmed from below using a mirror. See text for details.

groups; Murray 1975), the fur-lined pouches of heteromyids effectively isolate dry food materials from the moist mucous membranes of the oral chamber. This prevents absorption of water by the food—water that would be lost to the environment when the food was later cached in the ground. Given the critical problems of water balance faced by desert heteromyids (see MacMillen, this volume), the savings potentially attributable to the use of external cheek pouches may be significant.

Previous workers have noted the speed with which desert heteromyids are able to collect and pouch seeds. Nonetheless, the speed of food handling has been quantified

only for the time required by *Perognathus* and *Dipodomys* to husk relatively large seeds (Rosenzweig and Sterner 1970). Some insight into the much more rapid process of pouching has been gained recently from high speed films made of an adult female *D. deserti* collecting unhusked millet and sunflower seed from a glass plate.

High speed pouching in *D. deserti* is highly stereotyped. Figure 2 illustrates selected stages in a typical pouching cycle. Both forelimbs move in synchrony and each limb serves only the ipsilateral pouch. At the initiation of the cycle the limbs are thrust forward and downward toward the seeds as the

hands are simultaneously pronated and opened (Fig. 2: F1-F18). The hands are next closed on the seeds and then retracted toward the mouth (Fig. 2: F18-F26). During the retraction stage the hands are supinated so that the palms face directly upward by the time the hands are below the pouch openings (Fig. 2: F26). The forearms are next elevated such that the fingers penetrate into the extreme anterior end of the openings (Fig. 2: F34). In the final stage of the pouching maneuver, the food is released and the hands are pulled downward away from the mouth ready to commence the next cycle (Fig. 2: F41).

The cine records reveal two additional aspects of the pouching mechanism. First, the reduced first digit (= thumb) is used in semi-opposable fashion. This small digit is held beside the large palmar tubercle and, hence, opposes the remaining fingers (II-V) when grasping food items. Second, the pouching cycle of the forelimbs is attended by synchronized mandibular movements. Each time the hands are drawn toward the pouches, the mandible is pulled rearward. Opening of the mouth at this time appears to allow the hands to enter the pouches while the pouch entrances are themselves kept tightly closed to prevent the exit of seeds already within them. The backward movement of the lower jaw appears to induce tension in the lips which, during pouching, are pursed behind the incisor teeth. The tension causes the lips to draw inward away from the lateral walls of the pouch, thereby creating small gaps at the extreme front end of the pouch into which the hands are thrust. As the mandible moves forward (= jaw closing), the pouch openings are again closed and the hands withdrawn.

Seed pouching in *D. deserti* is rapid, with a mean pouching rate for millet seed of 9.01 cycles per second. Some cycles are executed in less than 90 milliseconds. Depending on how many seeds are grasped in each hand, pouching rates range between approximately 20 and 60 millet seeds sec^{-1} . Though the conditions under which these values were obtained are admittedly artificial, they indicate the potential speed and efficiency of the pouching mechanism of *Dipodomys* under favorable circumstances. Unfortunately, com-

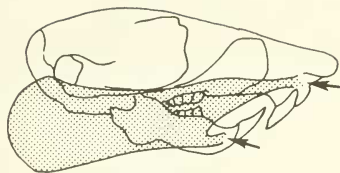
parable data are not yet available for *Perognathus* and *Microdipodops*.

Our films also hint at the mechanism by which kangaroo rats distinguish between edible and inedible items during high speed pouching. In no instance were unacceptable items recognized and rejected while in the hands. The films suggest that pouch items are quickly tested for suitability before pouching by being pinched between the pursed lips or, in the case of large items (sunflower seeds), between the lower incisors and the lips. Pinching of the food appears to be another consequence of the coupling of mandibular motion to forelimb movement. Those items judged unacceptable by the "pinch test" are then retrieved from the front end of the pouch and thrown backward beneath the animal.

Mechanical Constraints

Pouch size is important in that it establishes the maximum quantity of food material that a heteromyid can transport. The relationship between pouch size and body size might therefore influence the foraging tactics of desert heteromyid rodents. To examine this issue, Morton et al. (1980) have recently measured mean pouch volume in 13 populations representing 11 species of heteromyids and one species of geomyid (*Thomomys bottae*). Volume was determined by filling the pouches of dead animals to near capacity with material of uniform size and density (unhusked millet seed; 0.71 g cm^{-3}) and then converting the weight of the contents to volume. These authors predicted that pouch volume (V_p) should scale as body mass (M_b) raised to the first power ($M_b^{1.0}$) using the standard allometric expression ($y = ax^b$). They argued that if this relationship existed, larger heteromyids could collect and transport more food relative to actual metabolic need ($\alpha M_b^{0.75}$) than small heteromyids. However, their prediction for the scaling of pouch volume to body size was realized ($V_p \propto M_b^{1.043}$) only when the sample was limited to small heteromyids ($< 30 \text{ g}$) and the much larger pocket gopher (116 g). They found no statistically significant relationship between pouch volume and body size within the genus *Dipodomys*. To explain this finding, Morton

A.



B.

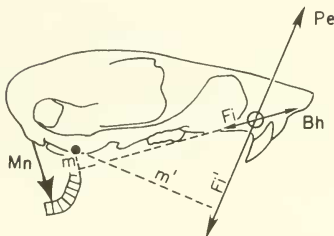


Fig. 3. A, Stylized illustration of anatomical relationship of external cheek pouch to head skeleton in *Dipodomys*. Principal anchorage of pouch (and contents) to skeleton is to rostrum and mandible at points indicated by arrows. B, Simplified diagram of mechanics of head stability under two locomotor conditions. In smooth bipedal hopping, acceleration of the head relative to pouch contents (Bh) is slight and has a largely horizontal trajectory. The opposing inertial reaction force (F_i) of the pouch load is also small and passes close to the fulcrum (dot) at the cranio-cervical joint. Accordingly, the force has a short moment arm (m) about the head-neck joint. The resultant destabilizing torque ($= F_i m$) (clockwise) is likewise small and is opposed by a counterclockwise torque supplied by the neck musculature (Mn). A much larger and more vertically oriented inertial reaction force (F_i') results from the rapid, steep trajectory of the head (Pe) as is occasionally seen during predator escape. This force has a large moment arm (m') about the fulcrum and therefore generates a much greater destabilizing torque on the head. See text.

et al. (1980) suggest that either relatively large body size, a preferred diet of high caloric seeds, and/or bipedalism may have released kangaroo rats from normal allometric constraints.

Several factors indicate that pouch volume might not increase as the first power of body mass. First, such a relationship implies the maintenance of geometric similarity, a pattern rarely encountered within a phylogenetic series encompassing an appreciable range of body size (Gould 1966). Second, in the analysis of Morton et al. an isometric relationship between pouch volume and body

mass was produced only when *Thomomys* was included, an inclusion that seems unwarranted in view of its systematic position, body plan, locomotor mechanics, and foraging behavior. Finally, biomechanical constraints may prohibit the maintenance of geometric similarity between pouch volume and body size in heteromyid rodents.

All desert heteromyids use some form of saltation, quadrupedal (*Perognathus*) or bipedal (*Dipodomys*, *Microdipodops*), when moving fast. Balance and stability are biomechanical problems that may increase with speed, especially if the gait involves rapid changes of direction. Several distinctive structural modifications of the neck in bipedal heteromyids appear to relate to the special problem of head stability (see earlier). The mass of the head will be a critical determinant of any stabilization mechanism. Moreover, the head must enter into any consideration of body balance (particularly in bipeds) since it is among the largest and heaviest structures forward of the point of limb support.

Anatomically, the cheek pouches are anchored to the head skeleton (Fig. 3A). At rest, much of the load provided by the pouch contents rests upon the back. However, during forward acceleration of the body, the load will tend to shift backward due to inertial lag. An appreciable fraction of this inertial force will act on the head. If the mouth is held closed, most of the inertial force acting on the mandible will be relayed to the rostrum of the skull through the masseter muscle. The inertial load from each cheek pouch can, for mechanical purposes, be regarded as concentrated at a single point well out on the rostrum (Fig. 3B).

The same figure illustrates the functional consequences of cheek pouch load under two locomotor conditions. In slow, smooth bipedal hopping, accelerational forces are small and the resultant inertial force is nearly horizontal. The line of action of this force passes close to the cervicocranial joint, thereby yielding only a modest destabilizing torque on the cranium. In the second case, that of escape from a predator, the animal accelerates very rapidly in a more vertical trajectory, similar to that recorded for *Dipodomys merriami* when avoiding the strike of snakes

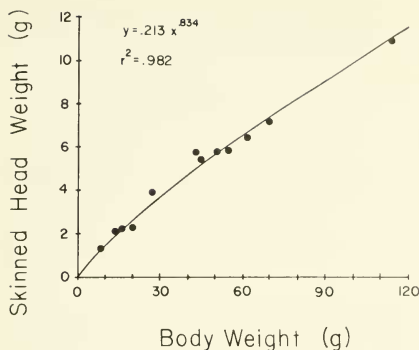


Fig. 4. Relationship of head mass to body mass in desert heteromyids (*Perognathus*, *Dipodomys*, *Microdipodops*). Negative allometry results in relatively heavier heads in smaller species. Restriction of the data set to bipedal forms gives the equation: $M_h = .270 \times M_b^{.776}$; $r^2 = .984$; $P < .001$, where M_h is skinned head mass.

(Webster 1961, Webster and Webster 1972) or for *Microdipodops* when escaping from another animal (O'Farrell and Blaustein 1974). Here the inertial force is much larger and passes further from the fulcrum between head and neck. Consequently, the destabilizing moment is much greater. The same inertial forces will also generate mechanical problems relative to body balance about the point of limb support in the bipedal pose.

Pouch loading can therefore have significant consequences for head stability and body equilibrium in heteromyid rodents, particularly during rapid escape maneuvers. This fact alone might preclude a simple isometric relationship between pouch volume (which is proportional to load) and body size. Because pouch load is coupled to the head, the manner in which head mass changes with body size might well reflect mechanical constraints that, in turn, influence the scaling of pouch size in desert heteromyids. Both head stability and body balance must be controlled even when the pouches are empty. Head mass scales as approximately $M_b^{0.834}$ in desert heteromyids and as $M_b^{0.766}$ when the data are limited to bipedal forms (*Dipodomys*, *Microdipodops*) (Fig. 4). Hence, larger heteromyids have relatively lighter heads than small ones.

If, in desert heteromyids, the scaling of head mass is associated with a constant level of function (i.e., stability and balance) with

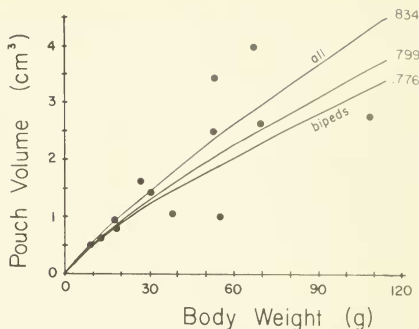


Fig. 5. Allometric relationship between pouch volume and body mass in desert heteromyids. Best least squares regression of standard allometric expression ($y = ax^b$) shows that pouch volume scales with strong negative allometry ($b = .799$) on body mass [$V_p = .085 M_b^{.799}$; $r^2 = .739$; $P < .001$]. The scaling of pouch volume is fairly closely predicted by the scaling of head mass to body mass in all desert heteromyids (all; $b = .834$) or just in bipedal forms (bipeds; $b = .776$). Taxa are identified in Fig. 6. Data from Morton et al. 1980.

the pouches unloaded, then continued functional equivalence will require that pouch load and pouch volume scale in the same manner as head mass ($= M_b^{0.83}$) if the density of the pouched material remains constant. The available data show that pouch volume goes as $M_b^{0.799}$ for desert heteromyids (Fig. 5). This is close to the prediction of pouch volume made on the basis of head mass (Fig. 4), and far from the original expectation of isometry ($M_b^{1.00}$; Morton et al. 1980).

Ecological and Behavioral Implications

The present model predicts that head mass and pouch load should scale isometrically with each other, but with negative allometry as regards body weight. The ratio of pouch load to head mass should remain fixed in desert heteromyids regardless of body size. The actual relationship is shown in Figure 6. If the model were correct, all points should fall on the horizontal line indicating isometry. Small heteromyids, in fact, cluster near the expected value except *Perognathus bail eyi*. However, the data for *Dipodomys* are scattered widely above and below the reference line. But the model predicts the relationship between pouch load and head mass

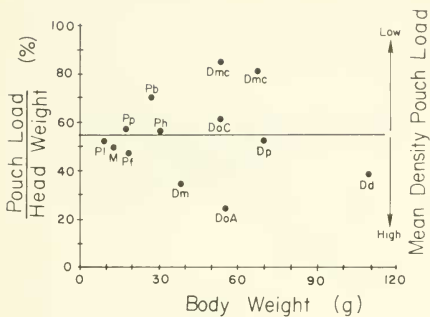


Fig. 6. Maximum pouch load as percent of skinned head mass in desert heteromyids of different body size. Load is based on maximal filling of pouches with unhusked millet seed. Data are derived from Morton et al. (1980). Each point is mean value for sample of that species or population. Maintenance of mechanical similarity among species requires that pouch load scale isometrically with head mass as indicated by horizontal line. Departure of points from this line may reflect natural differences in foraging behavior and dietary preference among the taxa, particularly as regards the average density (mass/volume) of the pouch load. See text for discussion. Taxa are: Dd, *Dipodomys deserti*; Dm, *D. merriami*; Dmc, *D. microps*; DoA, *D. ordii* (Arizona); DoC, *D. ordii* (California); Dp, *D. panamintinus*; M, *Microdipodops megacephalus*; Pb, *Perognathus baileyi*; Pf, *P. furnosus*; Ph, *P. hispidus*; Pl, *P. longimembris*; Pp, *P. parvus*.

only. It can predict pouch volume only if the physical properties (size, shape, density) of the food filling the pouches are the same for all species. This requires, in effect, that all desert heteromyids utilize identical food resources, a requirement clearly at odds with the actual foraging patterns of these animals (see Reichman, this volume).

Because the data illustrated in Figure 6 were obtained by filling the pouches with a uniform material (millet seed), the scatter of the points directly reflects interspecific or populational differences in relative pouch volume. Those taxa above the reference line have relatively large pouches; those below, much smaller pouch volumes. To conform to the model, species with larger pouches must, in nature, fill them with lighter materials than those below the reference line. What Figure 6 offers, then, is a graphical indication of qualitative and quantitative differences in pouch contents. It suggests, for example, that *Perognathus baileyi* typically harvests and transports relatively lighter food items than

the other *Perognathus* included in the sample. Similarly, the high degree of scatter within the genus *Dipodomys* should reflect considerably greater diversity in foraging behavior as compared to *Perognathus*. The least dense pouch materials are predicted in *D. microps*, an expectation not inconsistent with its tendency toward herbivory (Kenagy 1972, 1973, Csuti 1979). By contrast, the maximum pouch loads of *D. merriami* and *D. deserti* should average 2.48 and 2.24 times denser than those of *D. microps*. Still more intriguing is the apparent disparity between the physical properties of the pouch materials in California and Arizona populations of *Dipodomys ordii*.

Several factors will determine the mean density of the pouch load. Included are the size, shape, and actual density of the individual food particles. Small, round, dense items (certain seeds) should yield the densest pouch loads. Larger or more irregularly shaped items of the same particle density will produce a lower density load. Bulky vegetation (including whole fruiting heads of flowers) will give still lower densities, because it does not pack tightly. Food handling behavior could also affect pouch load. For example, a rodent that husks seeds prior to pouching them is creating a much denser pouch load.

Two additional behavioral-ecological predictions derive from a consideration of biomechanical constraints imposed by pouch loading. The first is that the right and left cheek pouches should be symmetrically loaded. This follows from the fact that mechanical stability of the head will be most easily maintained if the weight is equally distributed, thereby providing for some measure of counterbalancing. Symmetrical pouch loading should be most critical to bipedal forms, less important in quadrupedal saltators (*Perognathus*) and of no consequence to fossorial geomyids.

Next, maximal filling of the pouches in desert heteromyids ought to be on the basis of weight and not volume. As is explained below, maximum pouch load is probably established with regard to predation risk. If the "full pouch" threshold were indeed triggered by weight and not volume, a kangaroo rat harvesting especially dense items might return to its burrow or caching area with the

pouches only partially filled. When gathering very light items, the same animal could conceivably fill its pouches to their volumetric limit without ever reaching the load limit.

The proposed connection between cheek pouch loading and predation again rests with simple biophysical considerations. Suppose a kangaroo rat is sifting the soil for seeds. If suddenly attacked, it will attempt to leap up and away to avoid capture. The rate with which the rodent accelerates away from the attacker is determined by the simple Newtonian relationship, $a = F/m$, where a is acceleration, m is the mass of the animal and F is the propulsive force applied to the ground. If F is the maximum force the rodent is capable of generating, it follows that maximum acceleration, maximum take-off velocity and maximum distance covered by the leap (holding take-off angle constant and ignoring aerodynamic drag) will decline in direct proportion to cheek pouch load. Hence, the acceleration of a loaded heteromyid is given by the expression: $a = F/(M_b + M_p)$, where M_b is the mass of the body and M_p is the additional mass added by the pouch contents.

If heteromyids load their cheek pouches in constant proportion to head mass (as argued above), the potential consequences for predator escape are easily ascertained. Among desert heteromyids the relative loss of acceleration due to maximal cheek pouch loading should scale as $M_b^{0.83}$ —i.e., as head to body mass. Small species will therefore be more adversely affected than large ones. All other things being equal, small heteromyids should be at greater risk from predation when transporting a full load in the pouches. If, for example, a 110 g *Dipodomys* and a 10 g *Perognathus* were both carrying pouch loads equaling 50 percent of head mass, the maximum rate of acceleration of the kangaroo rat would be lowered by 4.6 percent and the pocket mouse would suffer a 6.8 percent loss of function.

The ability of heteromyids to accelerate sharply is undoubtedly a key element in their defense against predators. Although vertical leaps and erratic changes of direction have been recorded for *D. merriami* (Webster 1962), during predator escape there is some evidence that *D. microps* run directly to a burrow or bush when suddenly startled

(Quinn 1983). Assuming that predation is a major factor in habitat selection, it is possible, therefore, that the relative effect of pouch load could influence their choice of microhabitat. Small species might be expected to forage preferentially in areas of close cover if exposure to predation and the distance to the nearest protection increases with the "openness" of the habitat. Within both *Perognathus* and *Dipodomys* the largest species should be able to successfully operate in the more open habitats since they are less handicapped by pouch load.

Strictly speaking, the model predicts differences in microhabitat availability, not their actual use. On biomechanical grounds large heteromyids are not necessarily excluded from areas of relatively close cover, but small species should be excluded from open areas. The range of microhabitats potentially exploited by heteromyids, with regard to the mechanics of predator escape, ought therefore to expand with increasing body size. This raises an interesting question with respect to *Microdipodops*, which is bipedal but also in the size range of *Perognathus*. At present there are insufficient data to compare the foraging tactics of *Microdipodops* with that of the smallest (but substantially larger) kangaroo rats (e.g., *D. merriami*, *ordii*). Theoretically, pouch loading should place a kangaroo mouse at greater risk in open habitats than even the smallest *Dipodomys*.

Unfortunately, we do not yet know how acceleration potential actually scales with body size in heteromyids nor how this potential compares with the speed of attack by natural predators. These and other confounding factors might conceivably alter expectations of habitat restriction drawn from simple biomechanical considerations. Still, the present model based on mechanical constraints offers straightforward predictions that are subject to testing.

FORELIMBS

The forelimbs of desert heteromyids have several functional demands placed upon them. Foremost among these are food handling and digging. They are also involved in body support and propulsion in *Perognathus*

at all speeds, but only at comparatively slow rates of travel in *Dipodomys* and *Microdipodops*.

Digging Activities

Nearly all small desert mammals live below ground at least part of the day, where soil acts as a buffer against temperature extremes and desiccation. Below 30 cm of sandy soil, soil temperature remains relatively constant throughout the day, despite fluctuations of 20 C or more at the soil surface (Kenagy 1973, Larcher 1980). Uniform temperatures throughout the year, however, are not achieved except at much greater soil depths. Most desert heteromyids dig elaborate multibranched burrow systems (Anderson and Allred 1964, Culbertson 1946, Quinn 1983, Vorhies and Taylor 1922) where they spend the day. Typically, they emerge above ground to forage only after sunset.

Dipodomys burrows tend to have multiple entrances, which are sometimes plugged during the day (Hawbecker 1940, Tappe 1941, Vorhies and Taylor 1922). They have a maximum depth of 30–75 cm (Anderson and Allred 1964, Culbertson 1946, Vorhies and Taylor 1922). The burrows of *Perognathus* tend to be less branched. Generally they have only one or two entrances and are rather deep, with nest chambers 85–193 cm below the surface (Eisenberg 1963, Kenagy 1973). Little is known about kangaroo mouse (*Microdipodops*) burrow systems, except that those of *M. pallidus* and *M. megacephalus* are short and simple (Eisenberg 1963, O'Farrell and Blaustein 1974), a fact that may minimize the energetic cost of torpor (Kenagy 1973).

The relative digging abilities of heteromyids has been given very little consideration. There is some evidence, however, that species may partition the land available on the basis of soil composition and particle size (Hardy 1945, Hoover 1973). Some species appear to be restricted to soft friable soils, but others are able to use harder, rocky soils. This would suggest that some species may be unable to dig in hard soils. Deynes (1954), however, found that *P. merriami gilvus* and *P. pennicillatus cremicus* were able to dig burrows in heavy clay-loam hard pan,

even though they are naturally confined to sandy soils.

Digging Methods

There are three main methods of digging utilized by heteromyid rodents. Very loose soils, such as dry, fine sand are often moved by pulling small piles of soil between the animals' hind feet using both front limbs simultaneously. These motions appear to be very similar to those of the forelimbs during high speed pouching of seeds. When a sufficient pile of soil has accumulated under the body, the hind limbs are used to kick the sand further back. This method of digging is used by *D. merriami* and *D. deserti* during surface foraging and in the initiation of new tunnels.

Soils of intermediate hardness are loosened by scratch digging techniques that employ the front limbs in an alternating pattern. This digging method is employed on the surface when burying seeds and foraging as well as underground when constructing or maintaining tunnel systems (Eisenberg 1963, 1975, Nikolai and Bramble pers. obsers). Soil loosened in this way may be moved with the hind feet by kicking or, when underground, the animal may turn around and push the soil with its forelimbs and chest (Eisenberg 1963). This latter method of transporting soil is invariably used to move soil up a tunnel ramp preparatory to plugging the entrance (Eisenberg 1963, Nikolai and Bramble pers. obsers). The soil is then usually patted into place with rapid alternating hand movements. Slow motion films show the frequency of such movements to be approximately 11.6 cycles per second in *Dipodomys merriami* and 5.5 cps in *Perognathus formosus* when working in damp sand (Table 1).

The third method of digging has been observed only in *Perognathus* on extremely resistant soils. Here the animal uses its incisors

TABLE 1. Digging rates for heteromyids in damp packed sand. See text for details.

Species	BW (g)	Digging (stroke/s)	Patting (stroke/s)
<i>P. longimembris</i>	10.0	4.00	—
<i>P. formosus</i>	21.1	2.55	5.5
<i>D. merriami</i>	42.0	7.58	11.6
<i>D. deserti</i>	115.0	5.27	8.23

to chew through cementlike soils (Deynes 1954). This digging behavior is similar to that seen in the closely related Geomyidae (Hill 1937). It is conceivable that mechanical restrictions on gape (Fig. 1) preclude this type of digging in *Dipodomys* and *Microdipodops*.

Limb Morphology

The forelimbs of *Dipodomys* and *Microdipodops*, like other bipedal rodents, are short compared to the hind limbs (Berman 1979, Howell 1932). Much of the reason for this seems to stem from the strong negative allometry of the hand relative to body size in bipeds as compared to the slight positive allometry in quadrupeds. The humerus is absolutely shorter in bipeds at all body sizes, but its length increases with body size at the same rate as in quadrupedal species (Table 4).

The tiny hands of *Dipodomys* and *Microdipodops* probably reflect specialization for high speed seed handling and pouching. Rapid food handling will, in turn, reduce the time an animal must forage beyond the safety of its burrow. The very high rates at which *D. deserti* pouches seed have already been mentioned. The small hands of the bipedal heteromyids may improve manual dexterity by providing a better fit between hand and small food items. Reduction of the hands may also facilitate high velocity movements of the forearms by reducing the moment of inertia of the distal limb segments. A reduction of mass will permit higher rates of cyclic oscillation without an increase in muscular force (i.e., energy expenditure).

The absolutely higher rates of limb oscillation in *Dipodomys* than in *Perognathus* while digging (Table 1) is somewhat surprising. Normally, maximum limb frequency would be expected to scale negatively on body mass, as does maximum stride frequency while running in quadrupedal mammals (Heglund et al. 1974). The reduced limb mass associated with the relatively smaller hands of *Dipodomys* is, however, unlikely to provide a complete explanation for its more rapid limb movements as compared to pocket mice. We suspect that the faster forelimb movements of *Dipodomys* may also be the product of historical selection for higher rates of food gleanings and pouching.

In desert heteromyids each of the four main digits (II-V) bears long, curved but thin claws. The claws are used extensively in burrowing but also appear to serve as winnowing rakes to snag seeds as the hands sift through fine sediment. The reduced first digit has a naillike covering. As suggested above, this finger seems to be semiopposable in *Dipodomys*; from its similar structure, the same function may be expected in *Microdipodops* and *Perognathus*.

The scapula and humerus of the bipedal heteromyids resemble, in several ways, those of highly fossorial mammals. The humerus is relatively short, stout, and wide across the distal epicondyles (Howell 1932). The ratio of epicondylar width to humeral length is about .30-.33 and .33, respectively, in *Dipodomys* and *Microdipodops* as compared to .34-.36 in the pocket gopher, *Thomomys*. The relationship is .23-.29 in *Perognathus*, a value similar to that of generalized quadrupedal rodents (.24-.28) and also close to the figures reported for *Heteromys* (.21) and *Liomys* (.26) (Wood 1935). The wide epicondyles of bipedal heteromyids and other digging mammals are associated with powerful extensor and flexor muscles of the wrist and hand as well as highly developed pronators and supinators of the forearm (Hildebrand 1982). The scapula of all heteromyids and geomyids has a distinct postscapular fossa (Hill 1937, Howell 1932). A similar fossa has been independently evolved in several groups of highly fossorial mammals (e.g., armadillos, badgers, etc.) and is functionally associated with an enlarged teres major muscle (Hildebrand 1982). This structural feature is but one of several that hint that the common ancestor of the Heteromyidae and Geomyidae was more fossorial than the more generalized living geomyoids (*Heteromys*, *Liomys*) would indicate.

In both heteromyids and geomyids the ability to pronate and supinate the forearm is especially well developed. This ability seems likely to be associated with the maneuvers required (see earlier) to effectively place materials in the cheek pouches. What deserves special notice are the structural specializations that permit such forearm mobility. Unlike most mammals in which pronation and supination involve chiefly long axis rotation of the radius, the movement is accomplished in geomyoid rodents primarily by

long axis rotation of the ulna and radius as a unit. Such exceptional motion of the ulna correlates with an extremely "loose" elbow joint in which the ulna is free to deflect inward and outward. A special check ligament connects the lateral epicondyle of the humerus to the lateral crest of the ulna. It prevents excessive medial deflection of the forearm on the humerus and serves to stabilize the otherwise weak elbow joint when the hand is flexed in the supine position (as in pouching and some digging maneuvers). The ligament cannot, however, strengthen elbow movements when the hand is pronated (palm down), as would be the case in quadrupedal locomotion. This raises the possibility that structural limitations may make bipedalism obligatory for larger desert heteromyids when running at higher speeds. The presence of a specialized elbow mechanism in heteromyids and primitive geomyids (*Thomomys*), together with its absence in selected representatives of other rodent families (i.e., Muridae, Sciuridae, Cricetidae, Zapodidae, Chinchillidae), indicates that the mechanism is derived for rodents but primitive for the Geomyoidea.

HIND LIMBS AND LOCOMOTION

The locomotor repertoire of heteromyids can be divided into two major classes: bipedal and quadrupedal. Both bipedal and quadrupedal heteromyids use quadrupedal gaits, such as the walk, half-bound and full-bound during slow progression. These gaits are very similar in their footfall pattern to the gaits used by other quadrupedal rodents (Gambaryan 1974). At higher speeds, however, some heteromyids (*Dipodomys* and *Microdipodops*) employ the bipedal hop, a gait that does not use the front limbs for support. Since much of the thrust of this gait is associated with dorso-ventral oscillation of the vertebral column, the bipedal hop is allied with the gallop as an asymmetrical gait (Badoux 1965, Hatt 1932, Howell 1965).

A question that has plagued researchers for some time is: Why did bipedalism evolve in some heteromyids and not in others? Bipedal locomotion seems certainly to permit greater specialization of the forelimbs for digging and food handling. Several researchers have

also suggested that bipedal locomotion is more energetically efficient than quadrupedalism (Dawson 1976, Dawson and Taylor 1973) or that bipedal locomotion is more effective in predator avoidance (Eisenberg 1975).

Based on energetics studies, Dawson (1976) has argued that small bipedal mammals, including heteromyids, are able to move faster using less energy than their quadrupedal counterparts. This suggests that quadrupedal heteromyids (such as *Perognathus*, *Heteromys*, and *Liomys*) might have foraging strategies that do not utilize high-speed running. Several ecological studies have been undertaken to test this idea (Reichman 1981, Thompson 1980, 1982a, 1982b).

A high-speed bipedal gait would be most effectively used by a small desert rodent to avoid predators (avian, mammalian) while moving from its burrow to a protected foraging site or from one site to another. Bipedal hoppers may also be more adept than quadrupeds at avoiding predators in open habitat due to the greater maneuverability and acceleration offered by the bipedal hop. Further, if bipedal hopping is energetically less costly than quadrupedal running, then maximum speed may be greater in bipedal hoppers than in similarly sized quadrupeds. These considerations seem to imply that quadrupedal heteromyids might be forced to confine their foraging to one or two shrubs close to their burrow entrance, but bipedal heteromyids may be free to forage under several more widely scattered shrubs. Thompson (1980, 1982a, 1982b) has compared the foraging behaviors of *D. deserti*, *D. merriami*, and *P. longimembris* (see Table 2), and his results seem to support this hypothesis.

The energetic cost of locomotion in kangaroos increases linearly with speed during quadrupedal (pentapedal) movement, but remains constant or may even decrease slightly during bipedal hopping (Dawson and Taylor 1973). This contrasts sharply with the pattern of quadrupedal mammals wherein the energetic cost continues to increase linearly at all speeds (Taylor et al. 1970). It has been suggested that elastic storage of strain energy in the muscles and tendons of the hind limb and back of kangaroos may be responsible for some of their "energy savings" (Alexander

TABLE 2. Comparison of foraging behaviors of bipedal and quadrupedal heteromyids.

Species	Estimated BW (g)	# Digs and gleans per minute	Average slow foraging speed (km/h)	Average transit speed between shrubs (km/h)	No. shrubs visited/ foraging hr	Maximum recorded speed (km/h)
<i>D. deserti</i>	110	5.00 ^a	1.25 ^a	6.33 ^a	8.7 ^a	26.7 ^a
<i>D. merriami</i>	36	5.99 ^a	.95 ^a	3.20 ^a	11.3 ^a	22.2 ^a
<i>P. longimembris</i>	11	.80 ^a	.61 ^a	1.76 ^a	1.8 ^a	—

^a(Thompson 1980)^a(Thompson, ms.)

and Vernon 1975, Dawson and Taylor 1973, Morgan et al. 1978). However, similar studies on small bipedal hoppers, such as kangaroo rats, have yielded conflicting results, with energetic savings indicated in some species (Dawson 1976) and not in others (Thompson et al. 1980, Thompson ms.). Moreover, recent work by Biewener et al. (1981) indicates that storage of elastic energy is not likely in the hind limbs of kangaroo rats due to the relatively thick plantar and achilles tendons.

Unfortunately, all studies of locomotor energetics in bipedal hoppers have utilized treadmills. Recent experiments have shown that the gait of *Dipodomys merriami* is substantially altered during treadmill running (Nikolai ms.). On solid ground, for example, stride length and stride frequency both increase with speed, but on treadmills the stride frequency remains relatively constant over a broad range of speeds. This, in itself, raises serious questions as to the validity of the energetic cost of bipedal locomotion in rodents as established by treadmill tests.

The speed at which gait transitions occur are also higher during treadmill than during overground running (Table 3). *Dipodomys merriami* utilize three distinct gaits on treadmills and on solid ground: (1) quadrupedal half bound, (2) tripodal half bound, and (3) bipedal hop. The tripodal half bound is a transition gait between the slower quadrupedal half bound and the faster bipedal hop, in which only one front limb is used for support during a locomotor cycle (Fig. 7). The use of the tripodal half bound as a transition gait is not completely understood, since by using only one front limb the impact load will be roughly double that where both front limbs are used. In any event, the use of short, relatively weak front limbs as effective shock absorbing devices appears to be limited to slower speeds.

The transition from quadrupedal to bipedal gaits is probably not equivalent to the trot-gallop transition of quadrupedal mammals (see Heglund et al. 1974). Because the half bound and bipedal hop are both asymmetrical gaits, the quadrupedal-bipedal transition speed should always be higher than the trot-gallop transition speed for a quadruped of equal body weight. Nonetheless, bipedal hoppers apparently use the quadrupedal half bound at speeds that a similarly sized quadruped, of normal limb proportions, would trot (Fig. 8). The trot may not be available to bipedal hoppers due to the difficulty of coordinating hind and forelimbs that differ greatly in length.

Impact loading of the forelimbs will increase as the inverse ratio of front limb to hind limb length in running mammals (Gambaryan 1974). When loading of the forelimbs reaches some critical level, bipeds then presumably switch to rear limb support. Therefore, the speed at which the gait changes from quadrupedal to bipedal should be lower in bipedal hoppers with relatively longer hind limbs. Likewise, bipedal hoppers with similar front limb length to hind limb length ratios should have quadrupedal-bipedal transition speeds that conform to a single allometric equation (Fig. 8). *Dipodomys*, which have front limb as a percentage of hind limb ratios of 38.0–43.3, have quadrupedal-bipedal

TABLE 3. Range of speeds for each gait utilized by *D. merriami* on treadmill and on solid ground.

Gait	Range of speeds	
	Treadmill (cm/s)	Solid ground (cm/s)
Quadrupedal half-bound	< 115	< 68
Tripodal half-bound	67–181	44–109
Bipedal hop	> 81	> 60

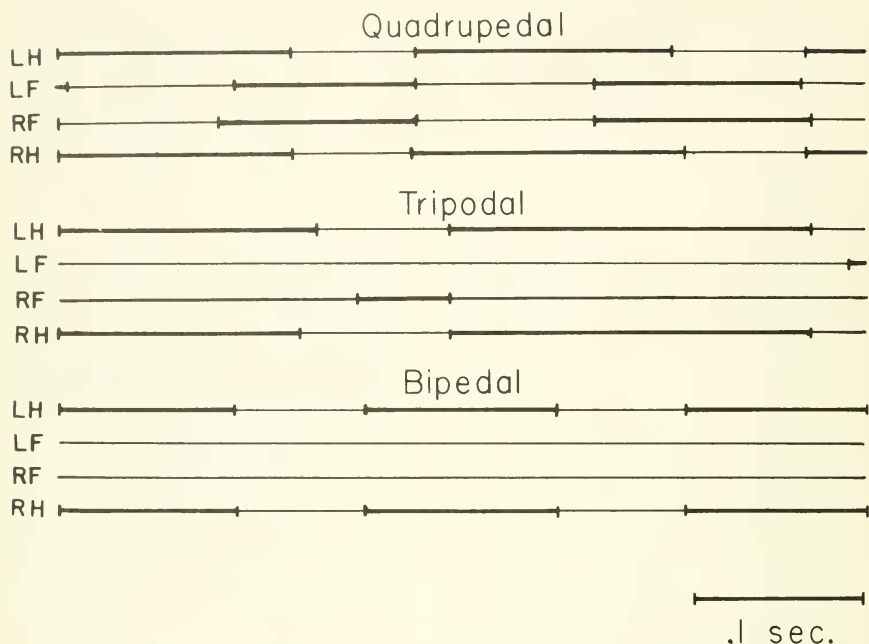


Fig. 7. Gait diagrams for *D. merriami*. Three representative gait diagrams depict the footfall patterns of the quadrupedal bound (top), tripodal half bound (center), and bipedal hop (bottom) at 60 cm/sec. During quadrupedal and tripodal locomotion, front limb support ends at touch-down for the hind limbs. Note that, although speed is the same for all three gaits, stride frequency is highest for the bipedal hop and stride length is greatest for the tripodal half bound.

transition speeds = $3.7 (\text{Body Weight})^{.178}$. *Perodetes capensis*, which is morphologically very similar to *Dipodomys* (Berman 1979), has a ratio of 35.4 and a quadrupedal-bipedal transition of 4 km/hr (Thompson et al. 1980), which is slightly lower than that predicted by the kangaroo rat equation. Kangaroos have ratios of 43.7–47.7 (Gambaryan 1974) and quadrupedal-bipedal transition speeds of 6.5 km/hr (Dawson and Taylor 1978). This is slightly above the value predicted by the *Dipodomys* equation (Fig. 8). Jerboas of the genus *Allactaga* have front to hind limb ratios of 27.5 (Gambaryan 1974) and therefore should have very low quadrupedal-bipedal transition speeds. The front limb to hind limb ratio of *Perognathus* (55.7–57.7) indicate that it would, in theory, be able to hop bipedally only at very high speeds. The limb proportions of *Microdipodops* (51.2) predict a relatively high quadrupedal-bipedal transition

speed, but well below that of a similarly sized *Perognathus*.

The ratio of forelimb length to hind limb length has been used extensively as an index of bipedality (Berman 1979, Howell 1932). It is clear that the hind limbs are elongated in bipedal hoppers and that most of the lengthening occurs in the distal segments (i.e., tibia and foot elements) (Berman 1979, Emerson ms., Howell 1932). However, whether or not the forelimbs are shortened relative to body size is the subject of some controversy (Gambaryan 1974, Howell 1932). Most osteological measures of animal size in common use (i.e., basicranial length, thoracolumbar length, body length) are greatly modified in kangaroo rats, and therefore of dubious value when making comparisons with more generalized rodent species. An exception to this is the length of the basioccipital bone of the skull, which appears to be relatively unmodi-

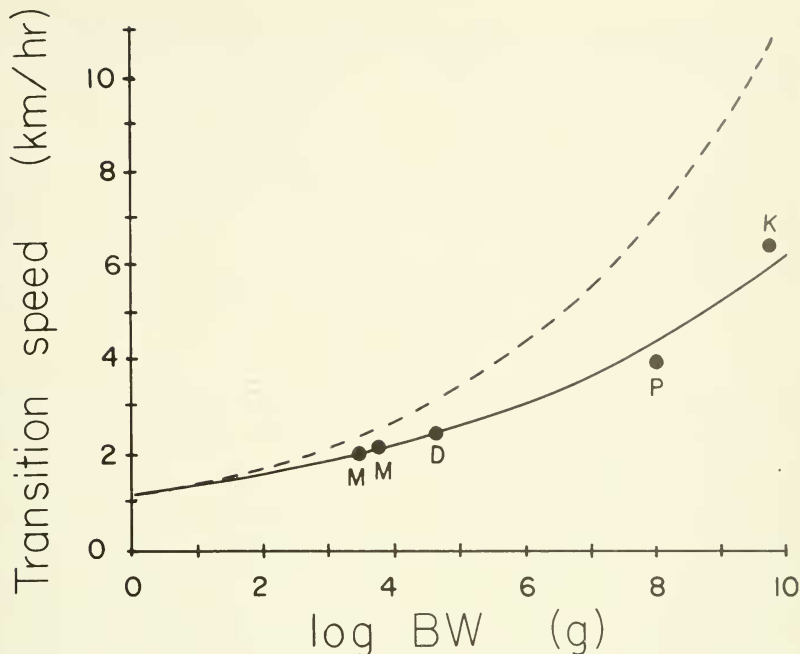


Fig. 8. Gait transition speeds. The trot-gallop transition speed for quadrupeds (dashed line) is $5.5 \text{ Mb}^{.24}$ (Heglund et al. 1974). The quadrupedal-bipedal transition speed for kangaroo rats (solid line) is $3.7 \text{ Mb}^{.178}$ (Nikolai ms.). The measured quadrupedal-bipedal transition speeds for bipedal hoppers are: (a) Red kangaroo (18 Kg), [K], 6.5 Km/hr (Dawson and Taylor 1973); (b) *Pedetes* sp. (3 Kg), [P], 4.0 Km/hr (Thompson et al. 1980); (c) *D. deserti* (.104 Kg), [D], 2.5 Km/hr (Thompson et al. 1980); (d) *D. merriami* (.0426 Kg), [M], 2.2 Km/hr (Nikolai ms.); (e) *D. merriami* (.032 Kg), [M], 2.0 Km/hr (Thompson et al. 1980). See text for details.

fied in kangaroo rats, as well as in many other mammals (L. Radinsky, pers. comm.). In desert heteromyids basioccipital length scales isometrically with body mass. We have therefore used this as a standard against which limb segment lengths are compared (Table 4).

The hind limbs of *Dipodomys* and *Microdipodops* are greatly elongated, and all three limb segments show strong positive allometry with respect to body size (Table 4). The foot and tibia are much longer in bipedal rodents than in similarly sized quadrupedal rodents, and there is a lesser difference in femur size (see also Berman 1979). It is interesting that as body size increases the relative length of the hind limb increases in bipedal heteromyids (*Dipodomys* and *Microdipodops*). This may have important biomechanical consequences. Since body mass scales as a vol-

ume and muscular strength as a cross sectional area (Alexander 1968), the ability of the leg muscles to absorb the shock of impact during bipedal hopping should decrease with increasing body size if geometric similarity is maintained. Increasing the length of the leg, however, will increase the contact time and thus the time course over which impact shock can be absorbed. The ratio of calcaneal length to total foot length also increases with body mass in bipedal hoppers [$= .09 + .514 \text{ Mb}$, $R^2 = .72$, $P < .02$ for 7 species of *Dipodomys* and *Microdipodops*], thus improving the mechanical advantage of the large ankle extensor muscles.

The vertebral column, pelvic girdle, and hind limb musculature of bipedal heteromyids are considerably modified compared to quadrupedal species (Berman 1979, Hatt 1932, Howell 1932). In general, the long

TABLE 4. Comparison of the allometric equations of limb segment length of bipedal heteromyids and quadrupedal rodents using basioccipital length as a standard unit of relative body size. See text for details. [Bipedal heteromyids: *M. megacephalus* (1), *D. merriami* (2), *D. ordii* (3), *D. microps* (3), *D. spectabilis* (1); Quadrupedal rodents: *P. longimembris* (1), *P. formosus* (3), *P. parvus* (2), *Thomomys* sp. (2), *Peromyscus* sp. (1), *Neotoma* sp. (2), *Eutamias* sp. (1), *Citellus* sp. (1)]. Number of animals in parentheses.

	Bipedal heteromyids	Quadrupedal rodents	ANCOVA	
			Power	Coefficient
Humerus	2.9 (B.O.) ^{1.17***}	4.1 (B.O.) ^{1.31***}	N.S.	°°°
Radius	3.0 (B.O.) ^{.85***}	3.7 (B.O.) ^{1.15***}	N.S.	N.S.
Hand	1.9 (B.O.) ^{.75***}	2.9 (B.O.) ^{1.11***}	°°	°
Femur	5.7 (B.O.) ^{1.29***}	5.1 (B.O.) ^{1.31***}	N.S.	°
Tibia	7.7 (B.O.) ^{1.19***}	5.8 (B.O.) ^{1.11***}	N.S.	°°°
Foot	8.6 (B.O.) ^{1.20**}	5.1 (B.O.) ^{.84***}	°°	N.S.

*p < .05

**p < .01

***p < .001

back muscles are greatly enlarged, the pelvic girdle-sacral joint is strengthened, and the cervical and thoracic regions are shortened. The major muscle masses of the hind limbs are concentrated proximally and become highly tendinous distally to reduce the moment of inertia about the hip joint during locomotion.

Experimental studies indicate that at lower bipedal speeds most of the thrust at takeoff is derived from the ankle and hip extensors. The ankle extensor muscles are larger and have greater mechanical advantage in *Dipodomys* and *Microdipodops* than in *Liomys* and *Perognathus* (Berman 1979). As speed increases, the role of the large back muscles, such as the longissimus series, increases with increasing back extension at takeoff. Based on angle measurements, knee extensors also play an increasing role at higher speeds (Biewenier et al. 1981, Pinkham 1976, Williamson and Frederick 1977). The quadriceps and hamstring muscles are probably important in shock absorption during landing. Some elastic storage may come from these muscles; however, this is probably not significant for kangaroo rats (Biewenier et al. 1981).

The tail of *Dipodomys* is elongated, with a rectangular cross section and a terminal tail tuft. It is used as a counter-rotator during bipedal locomotion to counteract the torque applied to the long axis of the body by the limbs. The tail reaches the highest point of its swing cycle just before touchdown. The strong tail depressor muscles (e.g., iliocaudalis, pubocaudalis, flexores caudae) pull the tail down during the contact phase so that the tail is at its lowest point just after take-off

(Fig. 9) (Nikolai ms.). The tail elevator musculature is linked to the large back extensor muscles in such a way that when the back is extended the tail is automatically elevated (Howell 1932). Most of the extension of the back occurs during the latter portion of the contact phase of a locomotor cycle; thus, when the tail depressor muscles are relaxed after takeoff, the tail is automatically elevated. Some elastic storage in the dorsal tail tendons seems likely. As the thrust of the hind limb increases with speed, the swing of the tail likewise increases to counteract torques about the center of mass (Fig. 9). During the quadrupedal half bound, the tail is limp and does not oscillate in the same manner as it does during bipedal locomotion (Nikolai, unpubl. data).

Foot length scales approximately isometrically with tail length in kangaroo rats [foot length = .36 (tail length)^{.944} R² = .923], but shows strong negative allometry in pocket mice [foot length = 1.29 (tail length)^{.635} R² = .945]. This implies that kangaroo rats maintain geometric similarity with respect to the tail and foot length, but larger pocket mice have relatively longer tails and shorter feet. This relationship in *Dipodomys* is consistent with the presumed importance of the tail as a counter-rotator during bipedal locomotion. It has been suggested that the tuft of hair on the tip of the tail is effective as a flag to distract predators during high-speed predator avoidance maneuvers. The tuft may also alter the aerodynamic properties of the tail so as to make it more effective as a rudder or counter-rotator during locomotion (Hatt 1932, Howell 1923).

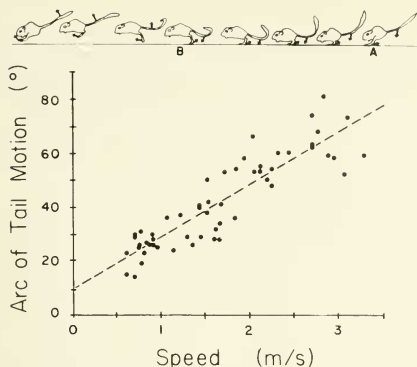


Fig. 9. Use of the tail in *D. merriami*. During bipedal hopping the long axis of the body shows very little rotation about the center of mass. During a locomotor cycle the legs exert a rotating torque on the center of mass (Pinkham 1976, Nikolai, unpubl. data). The rotation of the tail is always in a direction opposite to that of the leg (as indicated by the arrows on the tracings of representative frames from a single locomotor cycle of a *D. merriami* traveling at 100 cm/sec on a treadmill). The tail reaches its highest point just prior to touch-down (A) and reaches its lowest point just after take-off (B). The maximum arc described by the base of the tail increases with increasing speed (dashed line) to counteract the torque applied by the legs. [Degrees rotation = $9.164 + 19.6$ (speed in m/s); $R^2 = .80$; $P < .001$; $N = 57$ for 2 *D. merriami* running on a treadmill] (Nikolai, ms.).

Limited data are available on the relative growth rates of the hind foot, tail, body length, and body mass for several species of desert heteromyids (Butterworth 1961, Chew and Butterworth 1959, Hayden and Gambino 1966, Lackey 1967, Reynolds 1960). However, to date there has been no real attempt to determine how: (1) ontogenetic scaling of body proportions relates to the development of bipedal locomotor ability during growth; or (2) ontogeny might provide a vehicle for morphologic adaptation in the evolution of bipedalism through heterochronic mechanisms (e.g., Alberch et al. 1979). We suspect that a closer examination of these issues might prove especially worthwhile.

Origins of Bipedalism

Why has bipedalism evolved in desert rodents? This is a persistent question for which three main explanations have been advanced: (1) to facilitate escape from predators (Bartholomew and Caswell 1951, Eisenberg 1975,

Hatt 1932); (2) to free the forelimbs for efficient food handling (Bartholomew and Carey 1954); and (3) to reduce the energetic cost of locomotion (Dawson 1976, Reichman and Obserstein 1977). As was indicated earlier, recent evidence appears to discredit the latter hypothesis, leaving only predation and food handling as alternative models. The two are, however, strongly interrelated.

Three general features describe bipedal rodents: (1) all inhabit (or forage in) relatively open habitats where the risk of predation is presumably high; (2) all are nocturnal; and (3) all tend to be solitary. The first factor has been much emphasized but may not, in fact, be the most critical. Other rodents, especially sciurids, successfully occupy open environments but none are bipedal. They are, however, mostly diurnal and often exhibit a high degree of sociality (Armitage 1981, Barash 1973, Sherman 1977). The close approach of a predator to such rodents is made difficult by intense illumination and the fact that the detection of predators is a responsibility shared by conspecifics within a living area. Some *Dipodomys* and *Jaculus* respond to novel objects and small predators in their territories by thumping the ground with the hind feet (Eisenberg 1975). Such behavior might conceivably alert nearby conspecifics of potential danger, but true alarm calls have not been reported for any bipedal rodent.

That a predator might more closely approach a solitary rodent at night seems highly probable. If so, its attack will be initiated at closer quarters, thereby demanding a more rapid and forceful response by the prey if capture is to be avoided. *Dipodomys merriami*, for example, appears to have little trouble in jumping away from the strikes of nearby rattlesnakes (Webster 1962, Webster and Webster 1972). Perhaps the most important advantage conferred by bipedalism is the ability to execute a rapid, controlled leap directly from a feeding (or pouching) posture. Virtually all quadrupedal rodents sit semi-erect while feeding or manipulating food with the forelimbs. When forced to flee, such animals must normally drop onto the front limbs before initiating a flat trajectory leap off the rear limbs. The brief time required to do this may be of small consequence to a

diurnal rodent but could easily spell the difference between capture and escape to a solitary, nocturnal animal in open terrain.

Morphological specialization for leaping among vertebrate animals invariably results in elongation of the hind limbs relative to the forelimbs (Berman 1979, Howell 1965). As a consequence, the forelimbs will necessarily incur higher mechanical stresses as they act as shock absorbers to break the fall of the longer, faster bounds generated by the rear legs (Gambaryan 1974). Stress on the forelimbs will be amplified if a high-speed bounding gait incorporates abrupt changes of direction, since the front limbs brake the forward momentum of the body as the turn is executed. Quadrupedal mammals with such gaits (e.g., cursorial lagomorphs, ungulates) exhibit extreme modification of the elbow to increase its resistance to injury. Long axis rotation of the radius and ulna is severely curtailed or eliminated (Hildebrand 1982, Howell 1965). This effectively precludes pronation and supination of the hands, making them nearly useless in feeding. In all bipedal rodents, by contrast, the hands are used extensively in feeding and digging. There has presumably been strong selection for the rapid, efficient use of the forelimbs in order to reduce foraging time. It is in this context that the evolutionary significance of bipedalism becomes clearer. This locomotor strategy seems to offer the only viable means of combining, in a single animal, limb specializations and functions which are otherwise incompatible.

The notion that bipedalism in rodents is directly linked to the occupation of open, arid habitats is seriously contested only by the modern Zapodidae. These rodents favor mesic, well-vegetated environments both in the New and Old worlds. Their possible relationship to the Dipodidae (Eisenberg 1981, Fokin 1978) as well as the presumed bipedal habits of *Zapus* would seem to make the locomotor behavior of these rodents of special value in unraveling the history of bipedalism in desert rodents. However, although *Zapus* is unquestionably capable of rapid, prodigious leaps, there seems to be no solid evidence that it is really capable of sustained, bipedal saltation. Slow motion films of *Zapus princeps* running and leaping on solid ground as well as on a

treadmill show that the forelimbs are involved in body support and shock absorption in every stride (Bramble and Nikolai pers. obs.). Further evidence of quadrupedal rather than bipedal bounding is found in the structure of the limbs. The forelimb-hindlimb length ratio of *Zapus* is similar to that of bipedal heteromyids (i.e., *Microdipodops*; Berman 1979), but the forelimb is constructed differently. Forelimb length relative to body size is comparable to that seen in generalized quadrupedal rodents. The hand is large rather than reduced, and there are no obvious specializations favoring pronation and supination of the forearm. We tentatively conclude that true bipedal locomotion probably does not exist in the Zapodidae and that leaping specializations of this group have little to do with the evolutionary pathways leading to bipedal saltation in modern desert rodents.

The development of bipedal saltation as seen in modern heteromyids cannot have been associated with the occupation of desert environments as we know them today. True deserts of North America appear to be of fairly recent origin (i.e., later Pleistocene; Van Devender 1977), whereas heteromyids exhibiting structural modification for bipedal saltation date from at least the later Miocene (Voorhies 1975, Wood 1935). Voorhies' (1975) recent suggestion that bipedalism may have first arisen among primitive dipodomys living in sandy, floodplain habitats deserves special consideration. Such restricted environments may occur within otherwise typical savannah habitat and may be relatively arid during periods of low rainfall. More importantly, sandy floodplains are frequently characterized by widely scattered vegetation and thus qualify as "open" habitat. If bipedal heteromyids arose under conditions such as these, their distinctive locomotor specializations may have considerably predated other specific adaptations (mostly physiological) to desert life.

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